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North American Late Devonian Cephalopod Aptychi

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Abstract

Enigmatic, flat body fossils have been collected from at least 9 localities in dark shales of Late Devonian age in northeastern Ohio. The fossils have been found mainly in the Cleveland Shale, a black shale interpreted to represent an anoxic environment, and more rarely in the Chagrin Shale, which was deposited in a dysaerobic environment. The benthic fauna of these shales is sparse and restricted. These Ohio fossils are comparable to similar structures found within the Woodford Shale of Oklahoma, a formation of equivalent age and depositional environment as the Chagrin and Cleveland shales.

The enigmatic fossil remains comprise at least seven authentic species referrable to the genus *Sidetes* Giebel, 1849. Five of these species are found in Ohio. *Spathiocaris tenuicosta* Cooper, 1932 is morphologically indistinguishable from *Sidetes chagrinensis* (Ruedemann, 1916), and is, therefore, placed in synonymy. Similarly, *Spathiocaris striatula* Cooper, 1932 is the junior subjective synonym of *Sidetes lata* (Ruedemann, 1916) and *Spathiocaris woodfordi* Cooper, 1932 and *Spathiocaris plicifera* Cooper, 1932 are junior subjective synonyms of *Sidetes newberryi* (Whitfield, 1882).

All of the fossils are extremely thin and, typically, flat structures marked with fine, nearly concentric, corrugations or folds and range from 0.7 cm to 8 cm in length. At various times they have been considered to be brachiopods, barnacle plates, cephalopod aptychi, or the phyllopod crustaceans *Spathiocaris* or *Aptychopsis.*

Scanning electron microscopy reveals no ultrastructure within the fossils. Electron-dispersive X-ray spectroscopy indicates they contain neither calcium, strontium, nor phosphorus. Brachiopods and arthropods from the same units do contain phosphorous. Their general morphology and ornamentation is also unlike that of brachiopods or arthropods, permitting their assignment to the Cephalopoda. They appear to be the aptychi of ammonites, structures which probably served as the animal's lower jaw. Their probable preservation as carbon films remnant of degraded organic material is consistent with what is known of cephalopod aptychi.

The reconstruction of two specimens that had been cracked and flattened during compaction shows the original form of the structures to have been broadly curved and scooplike. This is consistent with reconstructions of Mesozoic ammonite jaws, and strengthens the assignment of these fossils with the cephalopods.

Introduction

In recent years there have been widely scattered reports of fossils believed to be cephalopod aptychi from the Paleozoic of North America (Brady, 1955, but see Yochelson, 1971; Closs, et al., 1964; Saunders and Spinosa, 1974; Saunders and Richardson, 1979; Thompson, et al., 1980; Yochelson, 1983; Kues, 1983; Mapes, 1987; Landman and Davis, 1988; Harper, 1989). Although several of these reports claim to be one of only a handful of such findings, many more specimens are available for study. The collections of The Cleveland Museum of Natural History contain over a hundred such specimens from the Late Devonian Chagrin and Cleveland shales.

These fossils are preserved as flat, glossy black, carbonaceous structures in the dark shales. They are marked with fine concentric ridges which parallel the margin or are truncated by it along the periphery. The ridges resemble those sometimes seen in brachiopods or bivalves, and the general outline could be suggestive of some early crustaceans. Similar fossils also have been identified as fish scales, barnacle plates, or perhaps gastropod opercula.

In the earliest description of these Devonian fossils in North America they were identified as a form of phyllocarid crustacean, *Spathiocaris* (Clarke, 1882). Woodward (1885), however, acknowledged that some "phyllocarids" could, in fact, be goniatite aptychi. Later, Clarke (1902) expressed doubts, admitting that they could be cephalopod aptychi or brachiopod fragments instead. This study was begun in an attempt to determine their affinities.

It was expected that the application of new methods might yield additional insight into the subject. Examination of the microstructure of these structures using the scanning electron microscope might reveal details of their formation and growth which would permit a more definitive identification. Determination of the chemical composition of these structures by x-ray spectroscopy might also confirm their affinities. Cephalopod shell material is aragonitic, whereas their mandibles are calcitic (Lowenstam, et al., 1984). Aragonite frequently contains strontium as a significant trace element. Inarticulate brachiopod shells and arthropod carapaces are composed primarily of calcium phosphate, not calcium carbonate. New chemical data would not necessarily be definitive, however, for bivalves are predominately aragonitic.

The principal purposes of this study are to examine and describe the "spathiocarids" of the Cleveland and Chagrin shales, investigate their relationships with similar Devonian taxa, and attempt to provide solid identification of their nature, if possible. This latter goal was not fully realized, but two of the most likely alternatives have been eliminated. It is probable that these fossils should be referred to the Cephalopoda.

Morphological Terminology

The terms describing the various forms of these fossil structures are complicated and somewhat confused. Many of the terms, originally defined as morphological features, have subsequently been adopted as taxonomic names. Further, a number of names of taxa have since been considered as morphological terms. It seems clearest to use the simple set of terms proposed by Moore and Sylvester-Bradley (1957a) in the *Treatise on Invertebrate Paleontology*. *Aptychus* (plural: *aptychi*) is considered to be a general name for this group of fossil cephalopod fragments, although it has a restricted meaning as the group of bivalved forms. *Anaptychus* is used to refer to the univalved structures found alone or in association with the pair of aptychi *sensu stricto* in younger rocks. For general discussion, these terms are useful:

"**aptychus** [broad sense] — All types of calcareous or corneous structures presumed to serve as opercula [or mandibles] of ammonoid conchs.

diaptychus [= aptychus *sensu stricto*] — Aptychus composed of two discrete valves.

anaptychus — Univalved type of aptychus." (Terms modified from Moore and Sylvester-Bradley, 1957a.)

With the multiplicity of interpretations, published descriptions of aptychi and similar specimens are hard to reconcile. The life orientation of these fossil fragments is necessarily different if they are arthropod carapaces (Clarke, 1882; Ruedemann, 1916), brachiopods (Clarke, 1902), cephalopod mandibles (Lehmann, 1970), or opercula (Trauth, 1927; Turek, 1978).

The orientation of these structures would be the same whether they were interpreted as crustacean carapaces or cephalopod mandibles. In each case, the rostrum or apex (center of the concentric ornamentation) is anterior; the hinged region is medial. The morphological terms used here (Figure 1) are based on those defined by Clarke (1962) for the description of coleoid cephalopod mandibles. The anterior angle is here defined as the angle of the anterior margin of the flattened fossil; convex if the rostrum is emergent, concave if it is reentrant.

Should it prove correct that aptychopsid plates were nautiloid opercula (Holland, et al., 1978; Turek, 1978) whereas aptychi proper served as ammonite mandibles (Lehmann, 1970), then new terminology would have to be created for the former. Not only would the function be different, but the two structures, otherwise similar in appearance, would have had opposite orientations in the living animals.

Previous Work

In 1847, C.G. Giebel reported the finding of some enigmatic fossil molds in the Cretaceous sandstones around

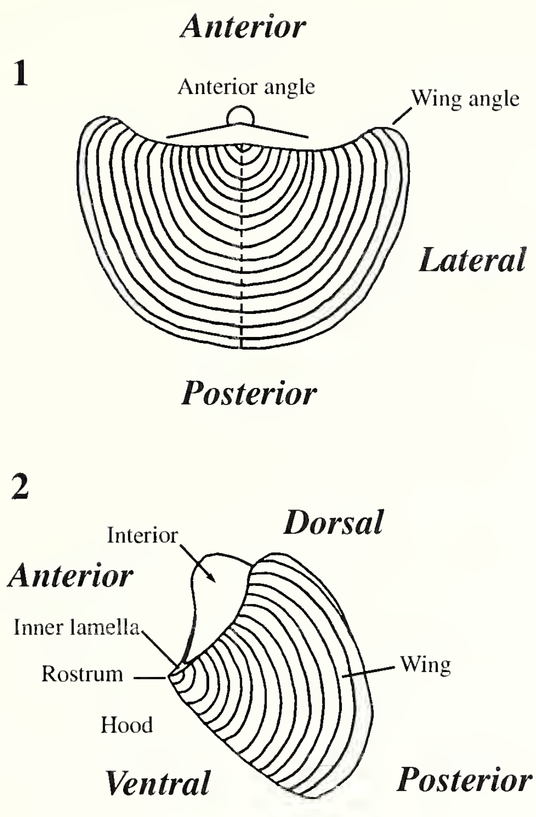

FIGURE 1. *Stylized diagrams of an early cephalopod lower mandible, showing reference attitude and morphological terms. Terminology after Clarke (1962).* 1, *Ventral view, extended and flattened.* 2, *Exterior lateral (oblique) view.*

Salzburg. He described the genus *Sidetes* Giebel, 1849, two years later, concluding that these structures were the aptychi of *Sepia* Linnaeus, 1758 (Giebel, 1849). The specimens he observed were semicircular, and marked with fine concentric lines.

Later, John M. Clarke (1882) described several odd fossils from Naples, New York, found in Givetian and Frasnian age shales of the Hamilton and Genesee formations. He collected thirty specimens over the course of several years, but remained doubtful as to their biological affinities. The fossils ranged in size from a few millimeters in breadth to as much as 90 mm, were flattened elliptical bodies marked with concentric lines or ridges, and bore a wedge-shaped cleft. He concluded they were not brachiopods as they were too large and did not display any trace of a corresponding ventral valve.

Clarke's descriptions were based on what he thought were incomplete specimens, consisting of isolated carapaces. He noted their general similarity to the Silurian arthropod genus *Discinocaris* Woodford 1856, and suggested these new specimens belonged properly with the phyllopod crustaceans, and that the discovery of a complete specimen would come with time. He assigned them to two crustacean genera, *Spathiocaris* Clarke 1882, and *Lisgocaris* Clarke 1882.

At the same time, Whitfield (1882) found similar fossils, which he referred to the crustacean genus *Plumulites* Barrande 1872. These specimens were all recovered from the Cleveland Shale in Erie County, Ohio.

Over the course of several decades of work with the British Museum, Henry Woodward had occasion to describe many small fossils of similar type. He proposed (Woodward, 1865; and see Woodward, 1885a) that some of these "ink-flecks" were chiton plates, while others were isolated barnacle plates, for which he proposed the genus *Turrilepas* Woodward, 1865. He subsequently (Woodward, 1882) referred similar specimens from the Devonian of Büdesheim, Germany to the new phyllopod genera *Cardiocaris* Woodward, 1882, and *Pholadocaris* Woodward, 1882, and a specimen from the Silurian of Wales to the phyllopod genus *Aptychopsis* Barrande, 1872. Later, he (Woodward, 1885) agreed that some such fossils may be cephalopod aptychi, but felt that others were certainly phyllopod carapaces.

Ruedemann's discovery, in 1901, of a very large brachiopod in the "Hudson river shales" [sic] of New York prompted Clarke to summarize 25 years of collecting *Spathiocaris* and similar fossils (Clarke, 1902). He observed that none had yet been discovered with abdominal fragments, and a specimen of *Spathiocaris* had been found in the body chamber of the Devonian goniatite *Manticoceras intumescens* in Germany (Kayser, 1882). He had earlier illustrated a similar occurrence of a "phyllocarid" *(Dipterocaris* Clarke, 1883) within a goniatite from the Naples (Portage) shales of New York (Hall, 1888, pl.35). His conclusions at this time were that *Spathiocaris* and similar forms were probably cephalopod aptychi, but that *Discinocaris* was perhaps a brachiopod. He gave this interpretation for the latter as its occurrence in the Silurian preceeded the appearance of the ammonites.

At about the same time, other dark shales were being studied. Girty's monograph (1909) on the Caney Shale (Devonian-Mississippian) of Oklahoma included a new genus, *Idiotheca,* which Girty hesitantly described as a conulariid. He briefly stated other possibilities, including its interpretation as a cephalopod aptychus. He ruled out the possibility of its being an inarticulate brachiopod.

Later, Ruedemann (1916) described four new species of *Spathiocaris* from New York and northeastern Ohio. He suggested several reasons to consider these fossils as belonging to the Cephalopoda, observing that the method of growth seen in *Spathiocaris* and related genera is similar to that seen in aptychi and not like that of brachiopods or arthropods. He supposed that the horny anaptychus would logically preceed calcareous diaptychi in the evolution of these structures, so the presumed lack of diaptychi from the Paleozoic does not mean that spathiocarids could not have been anaptychi. Finally, he suggested that similar structures would, "also have existed in the Ordovician and Silurian cephalopods and thus account for those earlier anaptychi considered as Discinocarina [sic]" (Ruedemann, 1916, p. 102).

Six new species of *Spathiocaris* were described by C.L. Cooper (1932) from the Woodford Formation of Oklahoma, including the redescription of Girty's *Idiotheca* specimen as the new species *Spathiocaris woodfordi*. The Woodford is an interbedded black shale/chert unit of Late Devonian to Early Mississippian age. Many of Cooper's descriptions are similar to species from the east. He described the fauna strictly as crustacean.

Ruedemann (1934) expanded upon the idea that *Spathiocaris* was a cephalopod aptychus, citing as evidence Matern's (1931) discovery of *Spathiocaris koeneni* Clarke, 1884 within the body chamber of *Crickites holzapfeli* Wedekind, 1913, a European Devonian goniatite. Ruedemann said it was unlikely that this represents the preservation of a phyllocarid preying upon a goniatite. The suggestion was made by Matern, and echoed by Ruedemann, that the anaptychi were separated from the conchs as the cephalopods decomposed while still buoyed by gases in the conch.

In his description of the New Albany Shale of Indiana, Campbell (1946) mentioned several thin beds within this Devonian black shale as "*Spathiocaris* beds." He suggested these horizons, where these fossils were locally abundant, might be useful in stratigraphic correlation. Unfortunately, such occurrences are too rare to be helpful (Lineback, 1970; Hasenmueller and Leininger, 1987).

Spathiocaris has also been identified in drill cores from western Canada (Copeland and Boulton, 1960), along with a phyllopod (crustacean) telson. This last has been removed from association with *Spathiocaris* and redescribed as *Montecaris* (Pratt, 1987).

Materials

Specimens in this study were collected by many different individuals from 1925 to 1989. Most were collected by P.A. Bungart or F. Thompson incidental to collection of Cleveland Shale fish material for The Cleveland Museum of Natural History (CMNH). All specimens studied were borrowed from The Cleveland Museum of Natural History, except for three specimens of *Aptychopsis* Barrande, 1872 which were kindly loaned by the Palaeontological Institute of Lund, Sweden (LO), Whitfield's type specimens provided by the American Museum of Natural History (AMNH), and Cooper's type specimens, which were borrowed from the National Museum of Natural History (USNM).

All the fossils studied from Ohio were preserved as carbonized films, flattened and compacted into the shale. Rarely was there a good interface between the specimen and the matrix, so preparation was held to a minimum. In a few cases folded specimens were separated from the rock along their outer surfaces. Most were prepared for photographic illustration by coating with finely particulate ammonium chloride. A few fragments were removed and coated with a thin film of gold for examination with the scanning electron microscope, but uncoated specimens were also examined by this technique with good results, probably due to their carbon content.

The USNM specimens, from the Woodford Shale of Oklahoma, are preserved as three-dimensional ellipsoidal packages of thin, sheetlike fossil material within phosphatic concretions from the shale matrix.

Stratigraphy and Localities

The fossils in this study have come from two units within the Late Devonian of northeastern Ohio; the dark colored Chagrin Shale and the overlying black Cleveland Shale (Fammenian). These shales are exposed along the southern shore of Lake Erie for 150 kilometers and extensively along many of the streams draining into the lake. The Devonian shale outcrop belt in northeast Ohio is illustrated in Figure 2, along with the known sites from which "spathiocarids" have been collected. These shale units represent prograding distal deposition of fine-grained sediments from the Catskill Delta to the east during a time of marine transgression in the Appalachian Basin (Lewis, 1988).

Prosser first used the name "Chagrin Shale" to describe the unit of interbedded gray shales and siltstones which Newberry called the "Erie Shale," as the latter term was preoccupied (Prosser, 1912, pp. 14-15). The unit is a wedge-shaped body thickening eastward into western Pennsylvania, where it is correlative with the Riceville Shale. It is underlain by the Huron Shale, another black shale. The Chagrin thins westward and pinches out east of the Huron River (Lewis, 1988). The Chagrin Shale consists primarily of greenish-gray or bluish-gray clayey shales interbedded with discontinuous siltstones. The shales frequently are bioturbated and often contain other traces of benthic life (Barron and Ettensohn, 1981; Hannibal and Feldmann, 1983; Schwimmer, 1988; Schwimmer and Feldmann, 1990). They represent gradual deposition within a dysaerobic low-energy environment (Barron and Ettensohn, 1981). The siltstones probably represent episodic storm events, washing coarser deltaic sediments westward in the basin (Hannibal and Feldmann, 1983).

The Cleveland Shale, named by Newberry in 1870, thins both eastward and westward from its maximum thickness west of Cleveland (Lewis, 1988). It consists primarily of black, laminated, fissile shales containing more organic matter and quartz and less clay (illite) than the gray shales of the Chagrin (Broadhead, et al., 1982). The lack of an

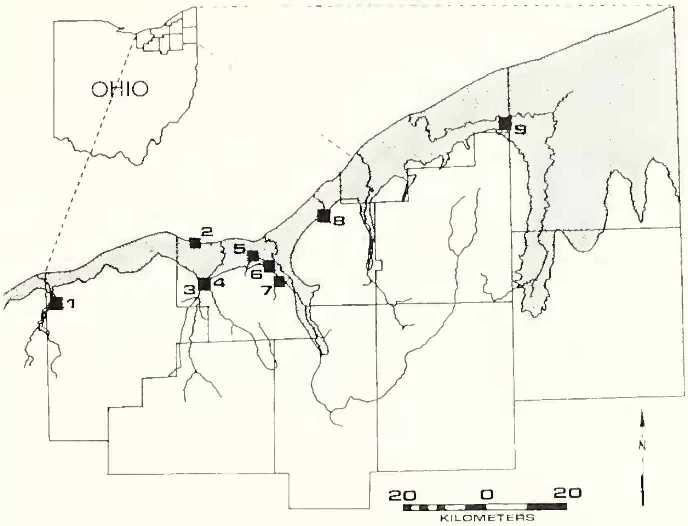

FIGURE 2. *Outcrop map of Devonian shales in northeastern Ohio. Numbered localities refer to sites where "spathiocarids" have been collected.*

active benthos and the enrichment in sulfides and organics indicates that the Cleveland Shale was deposited in deeper, anoxic conditions (Barron and Ettensohn, 1981). While it lies over the Chagrin Shale, there is a general east-west transition between the two units as the gray Chagrin grades westward into the black Cleveland Shale (Prosser, 1912; Szmuc, 1970a). The Cleveland Shale is overlain in turn by the Bedford Formation. The contact is sharp but conformable, marked by a thin bed of pyritized brachiopods and vertebrate fragments (Szmuc, 1970b).

Localities

The known localities at which these fossils have been found are listed here, in order from west to east. The numbers correspond to those in Figure 2.

1) *Chance Creek* — An easterly tributary of the Vermilion River in Lorain County. Kipton 7.5 Minute Quadrangle, Brownhelm Township, T6N, R19W, 41°21′40″N, 82°18′00″W. Exposures occur on Chance Creek, 400 m south of the intersection of Vermilion Road and Gifford Road. The Cleveland Shale in this region is approximately 15 m thick (Lewis, 1988). Specimens CMNH 3744, 3746, and 3747 were collected by William J. Hlavin from a zone 0.5 to 1.5 m below the Cleveland-Bedford formational contact. "The base of the invertebrate zone is characterized by a thin bone bed which contains water-worn, disarticulated elements and teeth of fossil fish" (Hlavin, 1976).

2) *Cahoon Cliffs* — Cliffs along the Lake Erie shore in Bay Village, Ohio. North Olmstead 7.5 Minute Quadrangle, T7N, R15W, 41°29′15″N, 81°55′30″W. The 10 m cliff east of the mouth of Cahoon Creek is an excellent exposure of the Chagrin Shale (Prosser, 1912). CMNH 6620 was collected as float along the beach, 100 meters east of the creek mouth.

3) *Little Cedar Point* — A bluff at the confluence of the East and West branches of the Rocky River. North Olmstead 7.5 Minute Quadrangle, T6N, R15W, 41°24′40″N, 81°53′20″W. The Cleveland Shale in this area forms steep, high cliffs along the river. The thickness of the unit appears to be 30 m, with the upper third somewhat more resistant than the rest (Prosser, 1912). Numerous concretions, cone-in-cone structures, and pyrite nodules have been found in the Cleveland Shale in this area. Forty-four specimens were located in the collections of The Cleveland Museum of Natural History in association with labels which read, "100 yds. E of ford at base of Little Cedar Point, 6/24/51" and "5/29/51, in a landslide." Although it is not clear which specimens, if any, are rightfully associated with these labels, the locality has been productive of both vertebrate and invertebrate material.

4) *Abram's Creek* — A southerly tributary of the Rocky River. Lakewood 7.5 Minute Quadrangle, T6N, R14W, 41°25′05″N, 81°52′00″W. CMNH 8312 was collected where Abram's Creek meets Rocky River, not far downstream from Little Cedar Point.

5) *Big Creek Localities* — Along Big Creek from Brookside Park to the Big Creek Metropark and beyond, the upper 30 m of the Chagrin and at least 15 m of the Cleveland are exposed. The Cleveland appears at the top of the cliffs on the south side of the creek just above Brookside Park; about three km upstream it reaches the stream bed south of West Park Cemetery, near the western edge of the Cleveland South Quadrangle (Prosser, 1912). Localities in the upper reaches of Big Creek include four along the northwest branch of the creek, and a region west of Linndale and north of Memphis Road. The fossils were collected as float and occasionally *in situ* in the creek bed. Lakewood 7.5 Minute Quadrangle:

- 5a) 30 m east of W. 140th St., T7N, R14W, 41°26′15″N, 81°47′30″W. CMNH 8317.
- 5b) First bend below W. 130th St., T7N, R13W, 41°26′15″N, 81°46′45″W. CMNH 8304.
- 5c) Above W. 128th St., T7N, R13W, 41°27′00″N, 81°46′45″W. CMNH 8303, CMNH 8315, CMNH 8316, CMNH 8318.
- 5d) At W. 117th St. T7N, R13W, 41°27′15″N, 81°46′00″W. CMNH 3745.
- 5e) Region of the Metropark north of Memphis Road, T7N, R13W, 41°23′45″N to 41°26′30″N,

81°45′15″W to 81°45′30″W. CMNH 7942, CMNH 8159, CMNH 8306, CMNH 8309, CMNH 8310, CMNH 8311, CMNH 8314.

6) *Brookside Park* — Located along Big Creek between the Big Creek Metropark and the creek's terminus at the Cuyahoga River. Trace fossils have been collected as float along the base of outcrops south of Big Creek in this area (Hannibal and Feldmann, 1983). Cleveland South 7.5 Minute Quadrangle, T7N, R13W, 41°26′30″N to 41°27′30″N, 81°42′15″W to 81°44′00″W. CMNH 8305, CMNH 8307, CMNH 8313.

7) *Skinner's Run* — On the border of Brooklyn Heights, Parma, and Seven Hills, Ohio. The Chagrin and the Cleveland are exposed along this tributary of the Cuyahoga River. At their contact is the Skinner's Run pyrite bed (Hlavin, 1976), a pyritized lag deposit enriched in fossils. Specimens were collected from the lower portion of the Cleveland Shale, somewhat above the pyrite bed. South central ⅑th of the Cleveland South 7.5 Minute Quadrangle, T6N, R12W, 41°24′30″N, 81°40′30″W.

8) *Euclid Creek* — East of Cleveland, in Euclid. The Chagrin Shale is exposed along Euclid Creek's west branch in the Euclid Creek Metropark. East Cleveland 7.5 Minute Quadrangle, T8N, R11W, 41°33′00″N, 81°31′45″W. CMNH 6576 was collected *in situ* north of a small gully extending from the park road, 1.8 km (1.1 mi) south along the park road from its intersection with Highland Road.

9) *Mill Creek* — Camp Stigwandish, Lake County, Ohio. The Chagrin Shale is exposed in the cliffs along this tributary of the Grand River. Thompson 7.5 Minute Quadrangle, T11N, R6W, 41°44′15″N, 81°02′00″W. CMNH 7948, collected as float from a steep cliff on the west side of the stream, 87 m upstream from the Doty Road bridge.

Systematic Paleontology

General

Aptychi present a particular problem to systematists. They are distinctive enough to be useful in stratigraphy, particularly where they are locally abundant enough to constitute "aptychus beds" (Campbell, 1946; Trauth, 1930). It is useful to be able to distinguish the forms by name, and indeed, many names were applied to these fossils by earlier workers before their nature was understood. However, the variability resulting from preservation and compaction has led to the erection of more species than was perhaps warranted (Turek, 1978).

As cephalopod conchs were discovered with associated aptychi, taxonomic conflicts arose; aptychus names often had priority over those well-known for the conch. Article 23 of the Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1985) would, in strict interpretation, have the earlier established name become that of the taxon, although section (b) of that article indicates that if this were to cause instability or confusion, an author can refer the case to the Commission for an individual ruling. In either case, one of the two names would have to be suppressed.

There is a complex heirarchy of ammonite taxonomy, based entirely on characters exhibited by the conchs. Aptychi do not possess sufficient morphological variation to permit diagnosis at the generic or specific levels. Thus in some cases, single "species" of aptychi have been found to belong to two or more genera of ammonites as distinguished by conchs.

A simple solution to this problem was proposed by Arkell (1954; 1957a). He favored the suppression of all names based solely on the aptychus of an ammonite. This proposal does assure the stability of ammonite nomenclature, at the expense of abandoning names useful for identifying aptychi as discrete entities separate from the remainder of the animal, as is often the case.

A more sweeping suggestion was made by Moore and Sylvester-Bradley (1957b) that a separate, parallel system of nomenclature be established for "parataxa;" names based on aptychi, individual conodonts, and isolated holothurian elements. In particular these names would compete with whole-animal names for the purposes of homonymy but not for priority. This proposal was fully supported by Arkell (1957b) as an extension of his original intent.

This parataxon proposal has provoked much debate, such that nearly thirty years later the question of parataxa has again been "put aside...for further in-depth study and future consideration." (International Commission on Zoological Nomenclature, 1985, p. xii). Until this question is resolved, the assignment of specimens to specific taxa is necessarily a cautious endeavour. Arkell (1957a) suggests using Trauth's (1927, 1928, 1930, 1931, 1935, 1936) system of nomenclature as form-genera only, while others simply refer to aptychi or anaptychi in general terms if association with specific cephalopods cannot be proved (Lehmann, 1971, 1981; Harper, 1989). Trauth's genera, however, are in many cases junior synonyms of older taxa. In this work, the taxa described for Devonian specimens will be considered appropriate, reserving "anaptychus" as a morphological term only. The "genus" *Anaptychus* Oppel, 1856, is an erroneous citation, as Oppel used the word merely as a morphological term describing the aptychus seen in *Ammonites planorbis* (citation of Oppel, 1856, in Moore and Sylvester-Bradley, 1957b). *Anaptychus* Stimpson, 1860 (Crustacea), and *Anaptychus* Schlumberger, 1868 (Cephalopoda), are junior subjective synonyms of *Sidetes* Giebel, 1847.

Class CEPHALOPODA Leach, 1817
Genus *SIDETES* Giebel, 1847

Anaptychus SCHLUMBERGER, 1868; *non* anaptychus OPPEL, 1856, morphological term; *non Anaptychus* STIMPSON, 1860, Crustacea.
Pholadocaris WOODWARD, 1882
Cardiocaris WOODWARD, 1882
?Ellipsocaris WOODWARD, 1882
Lisgocaris CLARKE, 1882
Spathiocaris CLARKE, 1882
Idiotheca GIRTY, 1909
Palanaptychus TRAUTH, 1927
Neoanaptychus NAGAO, 1931

Type species
Sidetes striatus GIEBEL, 1849.

Diagnosis
Semielliptic carbonaceous structure, weakly convex. Ornamentation of fine concentric lines about a medial anterior (by definition) rostrum, parallel to posterolateral margin, intersecting anterior margin at nearly right angles.

Description
Structure semielliptic, length 22 mm, weakly convex. Broad, width twice length. Anterior margin straight. Posterior margin smoothly curved. Ornamentation concentric with posterior margin, perpendicular with anterior margin, finely spaced at about 15/cm. Composition carbonaceous, probably conchiolinous, with no evidence of calcareous component.

Locality of type species
Unknown, "from hard sandstone banks near Salzburg" (Giebel, 1849). Age is Late Cretaceous (Senonian).

Type
Location unknown.

Remarks
Five species of *Sidetes,* described below, are recognised from the Ohio Shale. All are preserved as carbonaceous films, compressed and flattened to varying degrees. None appears to be accompanied by a calcitic or aragonitic component. All have a roughly semielliptic outline, and bear concentric ornamentation which terminates at the anterior margin in a manner unlike that of brachiopods or bivalves.

The specimens described by Cooper (1932) have been reexamined, as they were collected from the time-equivalent Woodford Shale of Oklahoma, a unit similar in character and depositional setting to the Cleveland Shale (Cardott and Lambert, 1985). The Woodford specimens are preserved in a different manner than the Ohio forms, however. They do not exhibit the extreme flattening common with the Ohio specimens, but are to varying degrees three-dimensional, with a significant mass of matrix material preserved within the interior of the structure, almost as a "steinkern." In general, they seem to have been preserved within calcareous or phosphatic concretions, a common alternative mode of preservation for [Upper-] Paleozoic aptychi (Mapes, 1987). All are similar to the Ohio specimens, with the addition of one species, *S. gouldi*, not recognised in the Ohio material.

Clarke's (1882) type species of *Spathiocaris* was *Spathiocaris emersoni*, originally described from New York. His original specimens have not been discovered. We were able to examine two specimens from Virginia (Butts, 1942), deposited at the National Museum of Natural History.

In his discussion of *Spathiocaris lata*, Ruedemann described transverse frontal grooves extending halfway to the anterolateral angles. These grooves caused him to, "recall those of the aptychus of some ammonites" (Ruedemann, 1916, p. 95). Such grooves are not seen in any specimen in this study. It is possible that they may represent in some manner a reflexed portion of the anterior margin analogous to the short inner lamella seen in anaptychus-type ammonite jaws from the Mesozoic (Lehmann, 1979; Kanie, 1982; Tanabe, 1983). Such structures may well have been obliterated in highly compressed material as is common in the Ohio Shale. Exterior molds, of course, would not reveal the inner lamellae. Finally, the Woodford Shale (Cooper, 1932) material has not been prepared to reveal the interiors of the convexly folded specimens, so such structures may well be preserved within the matrix which remains.

The species are differentiated on the basis of the ratio of breadth to length, the angle of the anterior margin, the general outline of the structure in its extended, flattened form, and, to a lesser degree, the nature of ornamentation. To this end, the following key is provided as an aid in species identification:

KEY TO DEVONIAN APTYCHI REFERRABLE TO *SIDETES*

1a) Width greater than length 2
1b) Width equal to or less than length 3

2a) Width twice length; ornamentation finely spaced, 16/cm .... *S. newberryi*
2b) Width about $^3/_2$ length; ornamentation coarse, about 8/cm .... *S. gouldi*

3a) Width half to $^4/_5$ length 4
3b) Width about equal to length 5

4a) Anterior margin acutely convex; outline elliptical .... *S. ulrichi*
4b) Anterior margin straight or broadly concave; outline triangular .... *S. chagrinensis*
4c) Anterior margin acutely concave, notched .... *S. emersoni*

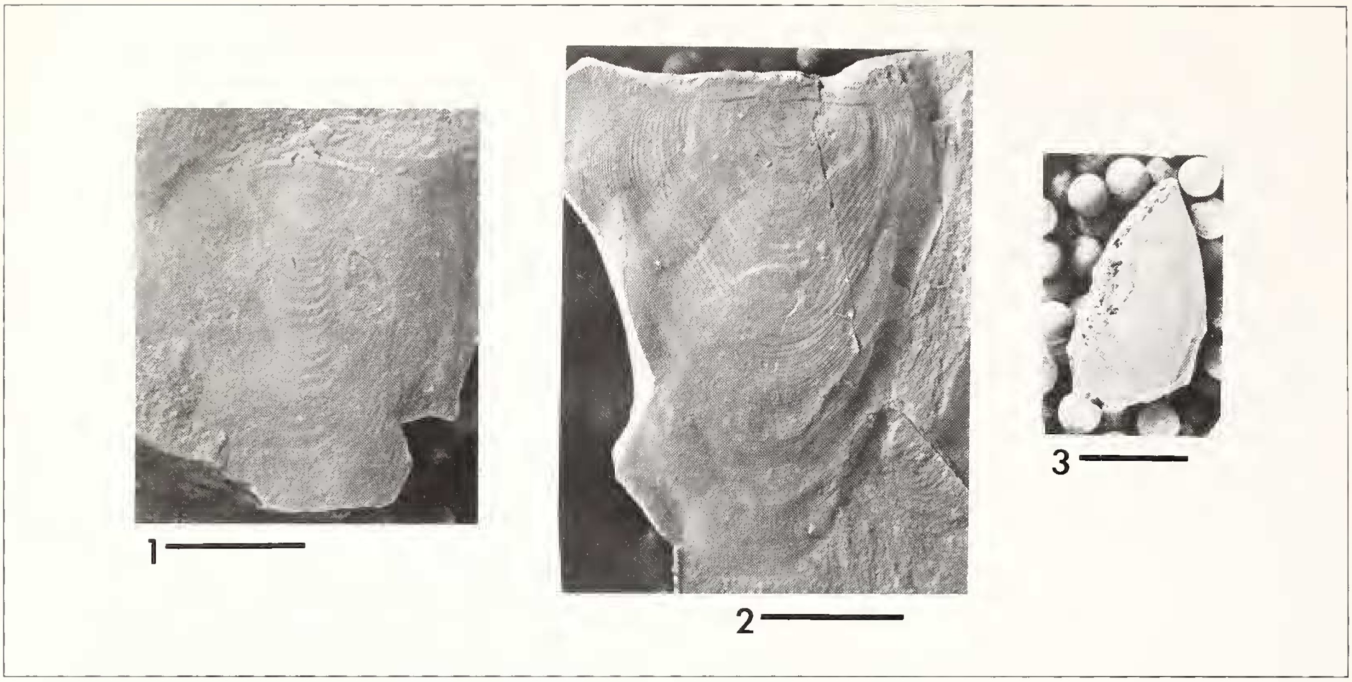

FIGURE 3. Sidetes chagrinensis *(Ruedemann, 1916).* 1, *Neotype, CMNH 3745, from Big Creek in Cleveland.* 2, *CMNH 3746, from Chance Creek in Lorain Co.* 3, *USNM 112031, from the Arbuckle Mountains of Oklahoma.* (Spathiocaris tenuicosta *Cooper, 1932). Scale is one centimeter.*

5a) Outline sub-pentagonal, lateral margins nearly parallel, meeting anterior margin at distinct angle .... *S. lutheri*
5b) Outline semielliptical, greatest width near anterior margin, narrowing posteriorly Anterior margin broadly concave .... *S. lata*

SIDETES CHAGRINENSIS (Ruedemann, 1916)
Figures 3.1 - 3.3

Spathiocaris chagrinensis RUEDEMANN, 1916, p. 95.
Spathiocaris tenuicosta COOPER, 1932, p. 350.

Diagnosis

Structure elongate semielliptical, length greater than width. Posterior margin strongly rounded and narrow; greatest width anterior near rostrum. Lateral margins but slightly curved, extending obliquely forward; anterior margin straight or broadly concave. Concentric ridges closely arranged, not very prominent. Fine longitudinal lines along hood radiate from rostrum to posterior tip.

Description

Fossil elongate semielliptical, appearing as a rounded isosceles triangle with base at anterior margin. Length about one quarter greater than width, ranging from 25 to 38 mm. Posterior margin strongly rounded and narrow, lateral margins slightly sinuously curved, extending obliquely forward to anterior margin, which is straight or slightly obtuse and concave. Concentric ridges closely arranged (14-28/cm), not very prominent. Fine longitudinal lines along hood radiate from rostrum to posterior tip, diverging slightly.

Type

Ruedemann's holotype was collected from the Chagrin Shale at Chippewa Creek in Brecksville, Ohio. It was in the Western Reserve University collection, parts of which have been transferred to The Cleveland Museum of Natural History. This specimen has not been located, however. For this reason, we designate CMNH 3745 as the neotype to serve in place of the missing holotype.

Material

Examined in this study were two specimens collected in June or July of 1965 by William Hlavin from the Cleveland Shale. CMNH 3745 is from Big Creek near W. 117th St. in Cleveland, and CMNH 3746 is from Chance Creek, Lorain County. Also studied were two specimens from the Woodford Shale assignable to this species, namely USNM 112031, Cooper's (1932) holotype of *S. tenuicosta*, and one of the paratypes of *S. gouldi*, USNM 112035, both from the Arbuckle Mountains of Oklahoma.

Remarks

Sidetes newberryi, *S. lutheri*, and *S. lata* are each broader than *S. chagrinensis*, with width/length ratios approximately one or greater. *Sidetes ulrichi* and *S. emersoni*, while also narrow, differ significantly in that the anterior margins are strongly curved rather than straight. Few specimens from the Chagrin Shale are well-preserved, and none of those now available represent this species. Even though the specimens in this study are from a different unit than the primary types, in all other respects they appear to conform to Ruedemann's description and illustrations of the species.

Cooper's (1932) species, *Spathiocaris tenuicosta*, differs from *S. chagrinensis* only in the manner of its preservation. It is folded along the median into a groove and ridge rather than a simple crease. In all other respects, it resembles the other specimens described here, and is properly assigned to *S. chagrinensis*.

SIDETES EMERSONI (Clarke, 1882)
Figures 4.1, 4.2

Spathiocaris emersoni CLARKE, 1882, p. 477.

Diagnosis

Structure semielliptical, length greater than width. Posterior margin rounded to subtriangular. Narrow, greatest width at anterior wing angle. Anterior margin deeply concave, notched. Concentric ridges closely arranged, well-marked.

Description

Fossils are semielliptical to subtriangular, width ⅔ to ⅘ length. Greatest width measured between wing angles, anterior of rostrum. Length ranges from 18 to 40 mm, width from 12 to 32 mm. Posterolateral margins straight to broadly curved. Ornamentation fine, about 20/cm, concentric with posterolateral margin, bending toward median at anterior margin. Anterior angle deeply concave, angle near 120°.

Types

Clarke's type specimens were from the Portage shales in Naples, Ontario Co., New York. They have apparently been lost. Two specimens collected by Butts (1942) and now in the National Museum of Natural History, USNM 97992-a and -b, are designated as "hypotypes."

Material

The specimens studied were the hypotypes, from Millboro, 1.6 km south of Shawver Mill, Virginia.

Remarks

Sidetes emersoni is narrower than *S. newberryi* or *S. gouldi*, while the deep anterior angle on *S. emersoni* differentiates it from *S. ulrichi*, *S. chagrinensis*, and *S. lata*. In outline, *S. emersoni* does not possess the sharp angle where posterior and lateral margins meet, as does *S. lutheri*, being instead nearly triangular.

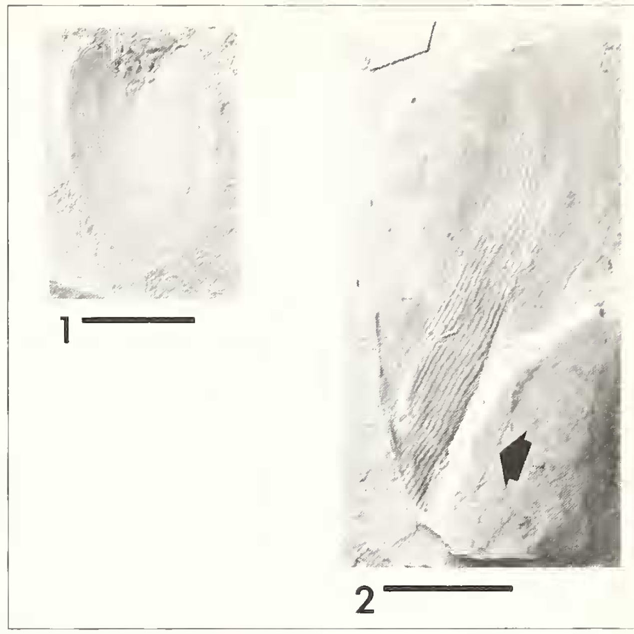

FIGURE 4. Sidetes emersoni *(Clarke, 1882). Hypotypes from Millboro, Virginia. 1, USNM 97992-a. 2, USNM 97992-b. Arrow points to fragment of opposite wing preserved on elevated portion of the matrix. Scale is one centimeter.*

It is interesting that none of the Ohio nor Oklahoma specimens can be assigned to this, the type species for the genus *Spathiocaris*. Only the one specimen of *S. lutheri* may possess an anterior margin as concave as *S. emersoni*. All other specimens studied have anterior margins which are less concave or even convex.

SIDETES GOULDI (Cooper, 1932)
Figures 5.1, 5.2

Spathiocaris gouldi COOPER, 1932, p. 349.

Diagnosis

Structure large, semielliptical, broad; width about 1.5 times length. Anterior angle straight or broadly concave. Ornamentation concentric with posterolateral margin, terminating anteriorly with inward bend toward median; spacing coarse, about 8/cm.

Description

Fossils are large, length about 40 mm; outline semielliptical; broad, width about 65 mm (1.5 times length). Anterior angle appears nearly straight. Ornamentation consists of ridges concentric with posterolateral margin, spaced about 8/cm. Anterior portions of ridges curve inward toward median.

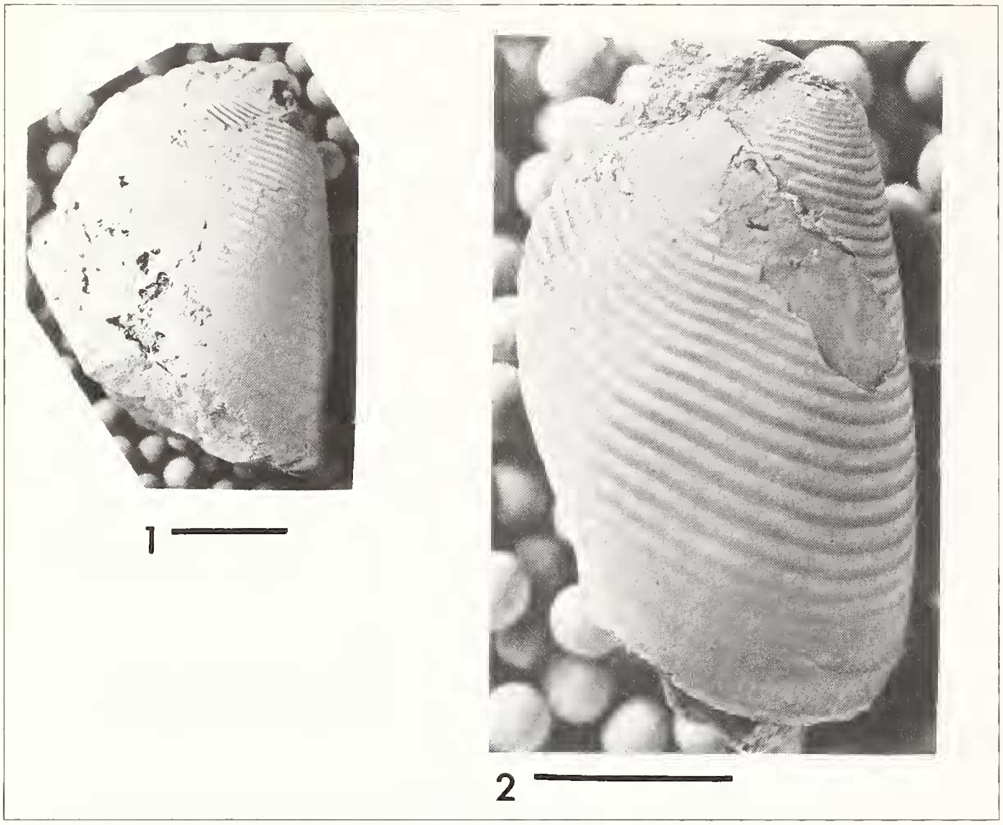

FIGURE 5. Sidetes gouldi *(Cooper, 1932), from the Arbuckle Mountains.* 1, *USNM 112023, holotype, from Sycamore Creek, OK.* 2, *USNM 112034. Scale is one centimeter.*

Types

Cooper's (1932) type material includes the holotype, USNM 112023, and a paratype, USNM 112034. USNM 112035, another paratype, is smaller and is ornamented with much finer ridges than the other two specimens. It is also much narrower in outline than the others, and properly should be referred to *S. chagrinensis*. The two type specimens definitely referrable to this species are from the Arbuckle Mountains in Oklahoma; the holotype was collected from Sycamore Creek.

Material

Specimens studied were USNM 112023 and 112034. None of the Ohio specimens of appropriate breadth exhibit ornamentation so coarse as to permit their assignment to this species.

Remarks

Sidetes gouldi and *S. newberryi* are the broadest species studied, all others being much narrower. *Sidetes gouldi* is slightly less broad than *S. newberryi*, which approaches a width/length ratio of 2 to 1. *Sidetes gouldi* is further distinguished from *S. newberryi* in that the ornamentation is half as finely spaced as that of the latter.

The two specimens have been removed from their surrounding concretions, and the anterior margins are poorly preserved, making determination of the anterior angle difficult. There is no indication, however, that it was significantly concave, but rather it appears to be nearly straight. While the spacing of the ornamentation near the rostrum frequently is finer than elsewhere on specimens of *Sidetes,* even this finer region is more coarsely ornamented than the ridges of *S. newberryi*, allowing easy distinction of the two species.

SIDETES LATA (Ruedemann, 1916)
Figures 6.1 - 6.7

?Cardiocaris lata WOODWARD, 1882, p. 388.
Spathiocaris lata RUEDEMANN, 1916, p. 94.
Spathiocaris striatula COOPER, 1932, p. 351.

Diagnosis

Structure semielliptical, length about equal to greatest width, which is near anterior margin. Anterior margin broadly concave. Ornamentation fine, concentric with posterolateral margin.

Description

Fossil semielliptical, posterolateral margin nearly circular or slightly flattened posteriorly. Greatest width, near anterior margin, approximately equal to length. Anterior angle broadly concave. Ornamentation fine, about 24/cm, concentric with posterolateral margin, bending toward median at anterior margin.

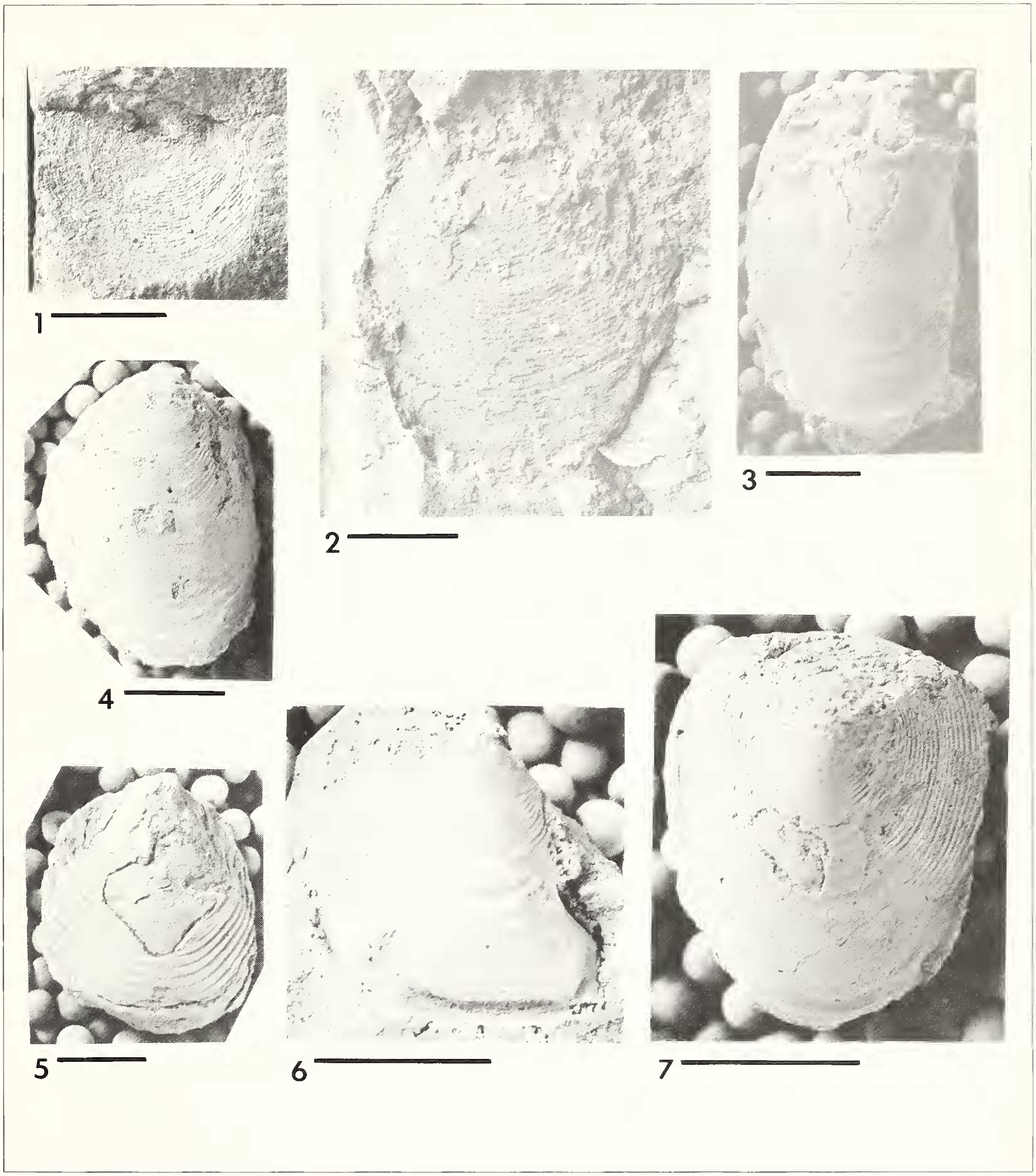

Figure 6. Sidetes lata *(Ruedemann, 1916).* 1, *CMNH 8313a, from Big Creek at Brookside Park, Cleveland.* 2, *CMNH 8307a, also from Big Creek.* 3, *USNM 112038, syntype of* Spathiocaris striatula *Cooper, 1932.* 4, *USNM 112032,* S. striatula *syntype.* 5, *USNM 112028* 6, *USNM 112029* 7, *USNM 112041. Scale is one centimeter.*

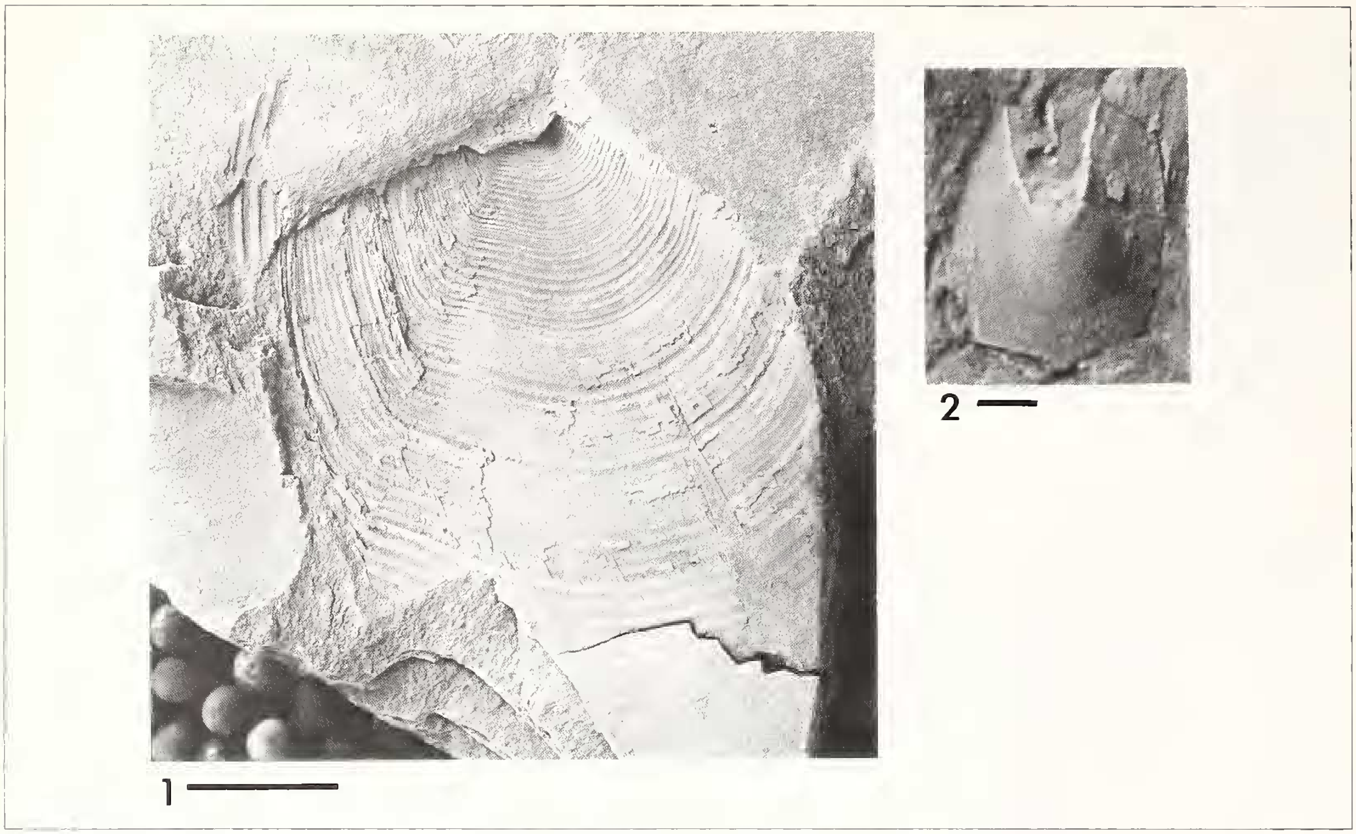

FIGURE 7. Sidetes lutheri *(Clarke, 1882). 1, CMNH 8302. Scale is one centimeter. 2, USNM 264093, the holotype. Scale is one millimeter.*

Type

Ruedemann's holotype was collected in 1895 from the "Chemung beds" near Avoca, Steuben Co., New York. It is now in the New York State Museum, NYSM 9860.

Material

Specimens studied which can be assigned to this species include CMNH 8307a and CMNH 8313a from Big Creek at Brookside Park. Woodford Shale specimens which can be assigned to this species are the type specimens of *S. striatula*, USNM 112038 and 112032, and three specimens formerly identified as *S. williamsi*, USNM 112037, 112029, and 112041. These last specimens do not conform with Ruedemann's description (1916) of *Spathiocaris williamsi*, being symmetrical and more narrow.

Remarks

Some specimens show superimposed, concentric undulations which are flatter and not as pronounced as those seen in *S. ulrichi*. *Sidetes lutheri* is distinctly different in outline from *S. lata*, while the other taxa are either decidedly narrower or significantly broader. Ruedemann described short carbonaceous lines radiating from a semicircular area at the anterior angle. These may be artifacts of preservation, as they have not appeared in any other specimen described from the North American Paleozoic.

Spathiocaris striatula was distinguished from the other Woodford Shale species by striations "radiating from the apex to the lateral and posterior margins of the shell" (Cooper, 1932). This feature is variously affected by preservation. Ruedemann (1916) noted imperfectly preserved striations in several species. Such striations are not seen in any of the Ohio specimens, but are present in several of the Oklahoma fossils, which are generally better preserved. The proportions of *S. striatula* and the ornamentation are identical with *Sidetes lata*, to which it should be referred.

SIDETES LUTHERI (Clarke, 1882)
Figures 7.1, 7.2

Lisgocaris lutheri CLARKE, 1882, p. 478.
Pholadocaris lutheri RUEDEMANN, 1916, p. 94

Diagnosis

Outline sub-pentagonal, lateral edges parallel, meeting posterior margins at sharp angles.

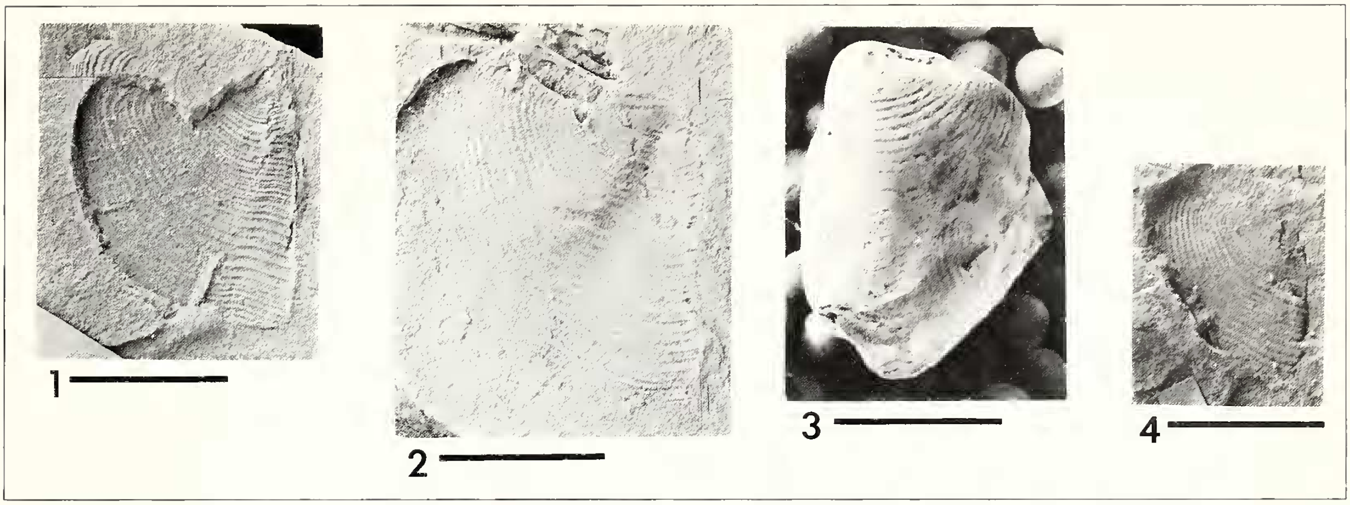

FIGURE 8. Sidetes newberryi *(Whitfield, 1882). Type specimens, from Erie County, Ohio. The remaining specimen in the type series is too degraded to reveal detail, and is not illustrated here.* 1, *AMNH CU 7452G.* 2, *AMNH CU 6686G.* 3, *AMNH CU 5513G.* 4, *AMNH CU 6063G. Scale is one centimeter.*

Description

Fossil large, length greater than 47 mm, width 43 mm. Outline sub-pentagonal; lateral margins parallel and meeting posterior margins at a sharp angle. Surface ornamented with concentric ridges parallel to margins, spaced about 16/cm. Ridges turn inward toward rostrum near anterior margin, which is not preserved.

Type

The holotype, USNM 264093, is in the collection of the U.S. National Museum. It was collected from near the base of the Hamilton Formation in Mile's Gully, Hopewell, New York.

Material

In addition to the holotype, one Ohio specimen was examined. CMNH 8302 was collected in 1938 by P.A. Bungart from an unidentifiable locality near Linndale in the Berea quadrangle map. No stratigraphic information was recorded.

Remarks

The unique outline and approximately equal length and width serve to distinguish *S. lutheri* from all other taxa in this study. Clarke's (1882) description of *Lisgocaris lutheri* was based on a single, very small specimen measuring only two by three millimeters. The distinctive configuration of the margins and concentric ornamentation, however, is maintained in the much larger CMNH specimen. Clarke described the species in reverse orientation to that given above, with an "abdominal" cleft beginning centrally and widening to the "posterior" margin. This anterior region is not preserved in the CMNH specimen, so the size and shape of such a cleft cannot be determined. There is evidence that the lateral margins extended anterior of the rostrum a slight distance, but whether the anterior angle was obtuse or acute remains unknown.

SIDETES NEWBERRYI (Whitfield, 1882)
Figures 8.1-8.4, 9.1-9.7

Plumulites newberryi WHITFIELD, 1882, p. 217.
Turrilepas newberryi HALL, 1888, p. 219-220.
Idiotheca rugosa GIRTY, 1909, p. 40.
Spathiocaris cushingi RUEDEMANN, 1916, p. 96.
Spathiocaris woodfordi COOPER, 1932, p. 351.
Spathiocaris plicifera COOPER, 1932, p. 350.

Diagnosis

Structure large, semielliptical, broad; width about twice length. Anterior angle straight or broadly concave. Ornamentation concentric with posterolateral margin, terminating anteriorly with inward bend toward the rostrum; spacing fine, about 16/cm.

Description

Structure large, length from 10 to 43 mm, semielliptical in outline, folded upon itself along the median line, forming a curved hinge. Broad, width 1.5-2 times the length. Anterior angle straight or very obtusely concave; anterior wings extend beyond hinge about one-fifth of total length. Entire structure extremely thin and flattened; in some specimens lateral margin is interrupted by one or more fissures, perpendicular to margin. Ornamentation of ridges concentric with posterolateral margin, spaced about 16/cm. Ridges continuous, terminating at anterior margin; anteriormost portion bent inward toward rostrum.

Types

Sidetes newberryi is the widest species herein studied. Only *S. gouldi* approaches it in width, but has much coarser ornamentation. All other species are rather narrower. Ruedemann (1916) described the new species *Spathiocaris*

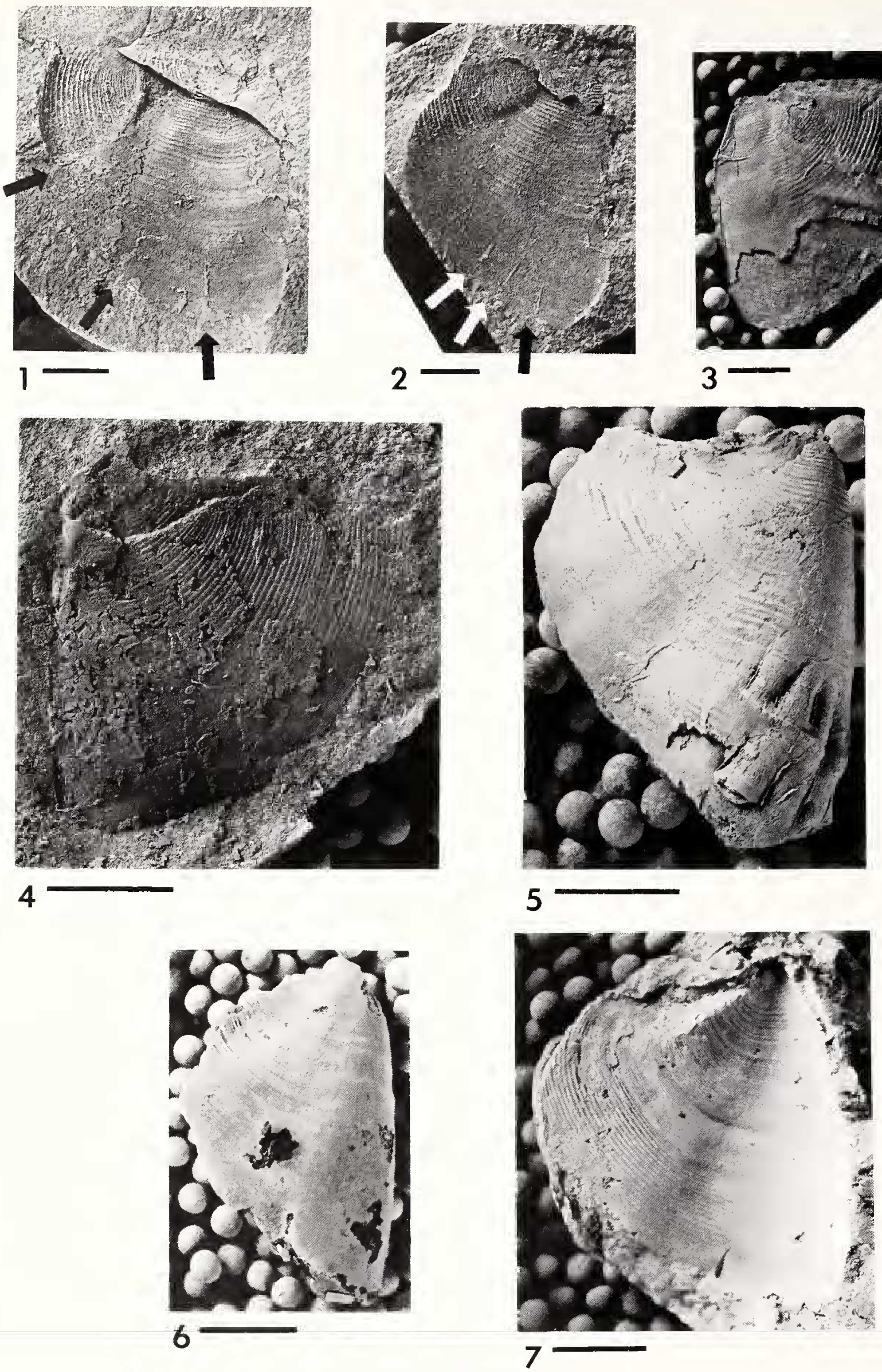

FIGURE 9. Sidetes newberryi *(Whitfield, 1882). Specimens from the Cleveland and Woodford shales.* 1, *CMNH 8311, and* 2, *CMNH 8318, from Big Creek, arrows showing fissures extending inward from posterior lateral margin.* 3, *CMNH 8320.* 4, *CMNH 8327a, with gypsum encrustation.* 5, *USNM 112030, holotype of* Spathiocaris plicifera *Cooper, 1932.* 6, *USNM 112040, and* 7, *USNM 112033, types of* Spathiocaris woodfordi *Cooper, 1932. Scale is one centimeter.*

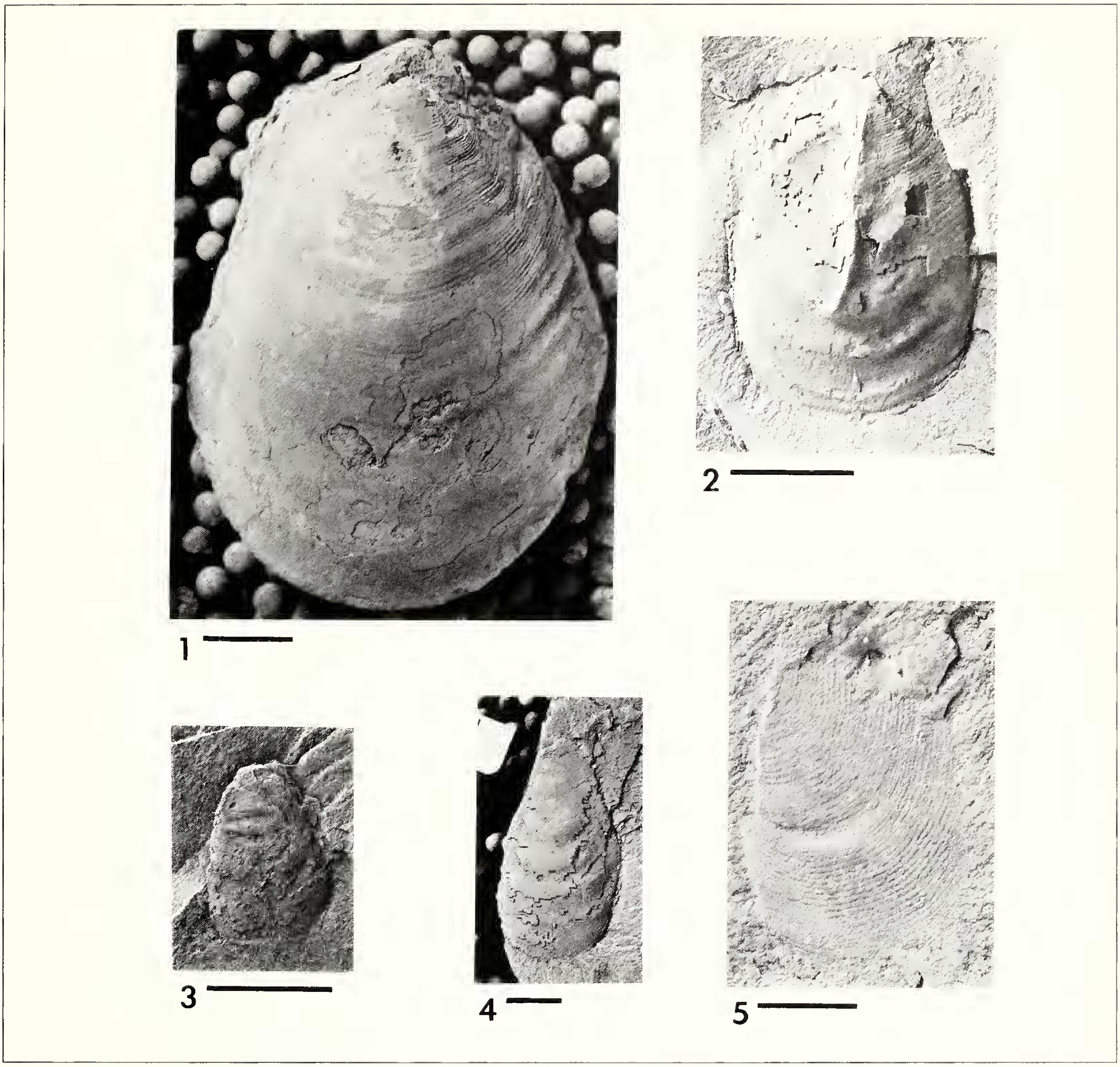

FIGURE 10. Sidetes ulrichi *(Cooper, 1932).* 1, *USNM 112036, the holotype.* 2, *CMNH 3744, from Chance Creek.* 3, *CMNH 8305b, also from Big Creek.* 4, *CMNH 8328a.* 5, *CMNH 8328b. Scale is one centimeter.*

cushingi based upon two specimens of *Turrilepas newberryi* collected from the Cleveland Shale. These specimens were part of the Western Reserve University collection, parts of which ar now at The Cleveland Museum of Natural History. These two specimens have not been located, however.

Whitfield's specimens of *Plumulites (Turrilepas) newberryi* are at the American Museum of Natural History (AMNH), and include the syntypes AMNH CU 7452G, AMNH CU 6685G, AMNH CU 6063G, AMNH CU 6686G, and AMNH CU 5513G. They were collected from the Cleveland Shale near Sheffield and Birmingham, in Erie County, Ohio. These agree in all details with Ruedemann's description and the specimens studied here, and do not exhibit the median carina nor multiple imbricate plates which might place them with the cirripedes. This species belongs with the aptychi.

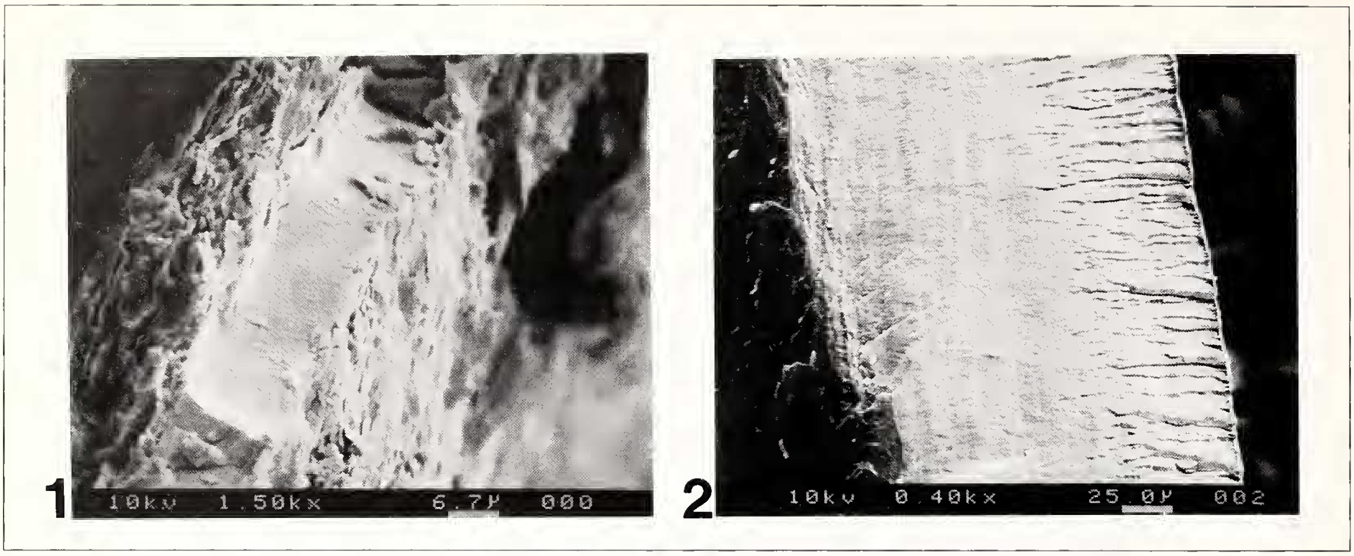

FIGURE 11. *Scanning electron micrographs of the cross-sections of the unmineralized wing area of cephalopod jaws. No internal structure is discernable in either specimen.* 1, Sidetes *sp. CMNH 8317, a presumed Devonian anaptychus.* 2, Nautilus pompilius, *a modern nautiloid. Scales are in microns as indicated. The Devonian specimen has been considerably compressed.*

Material

Material studied includes Whitfield's five specimens of *Turrilepas*, CMNH 8311 and CMNH 8318, from Big Creek, collected as float material, and CMNH 8312, from Abram's Creek. CMNH 8320 and CMNH 8327a, also studied, have no reliable collection data recorded. Ruedemann's types were collected by Professor H.P. Cushing from the Cleveland Shale along Cahoon Creek, not far from Cahoon Cliffs. One specimen, CMNH 8668, has been found within the old Western Reserve University collection, but it does not appear to be one of Ruedemann's type specimens. Woodford Shale material assigned to this species are Cooper's (1932) types of *S. woodfordi*, USNM 112033 and 112040, and the holotype of *S. plicifera*, USNM 112030.

Remarks

Ruedemann's description of *Spathiocaris cushingi* included mention of a second set of concentric lines centered upon the wing angles of the valve. This set "is but faintly shown" in the second, larger specimen he described, and may be invisible depending on preservation. Its absence should not rule out the assignment of the CMNH specimens to this species. Girty (1909, p. 40) illustrated a new genus and species of Pteropoda, *Idiotheca rugosa*, from the "Woodford chert" [sic] at the base of the Caney Shale (Devonian-Mississippian) in Oklahoma. He was uncertain of its affinities, granting that it "may possibly be an aptychus…which occur so abundantly at a little higher horizon…" (Girty, 1909). Cooper (1932) redescribed the same specimen, USNM 112044, along with another, USNM 112033, as the new phyllocarid species *Spathiocaris woodfordi*. His *Spathiocaris plicifera*, holotype USNM 112030, differs from the rest only in preservation, bearing secondary corrugated folds. These Woodford Shale specimens are indistinguishable from *Sidetes newberryi*, and belong within this taxon.

Ruedemann (1916) also described another species from the Cleveland Shale along Mill Creek in Newburg, Ohio (Cleveland), *Spathiocaris williamsi*, which may represent another folded specimen with a hinge more strongly curved than *S. newberryi*. He described *S. williamsi* as being asymmetrical and having the apex or rostrum displaced to one side of the "median line." This asymmetry is suspect. If we consider the lateral margin of his specimens nearest the rostrum to be the folded hinge line of a compressed specimen, the half which remains visible strongly resembles *S. newberryi*. Possible differentiating features might be coarser ornamentation (about 10/cm) and a superimposed concentric furrowing with a spacing of about 3-4 mm. Insofar as Ruedemann's types have not been located for study, it seems prudent to consider the two taxa as separate.

SIDETES ULRICHI (Cooper, 1932).
Figures 10.1 - 10.5

Spathiocaris ulrichi COOPER, 1932, p. 352.

Diagnosis

Structure sub-elliptical, narrower at rostrum. Anterior margin acutely convex. Broadly convex, highest point

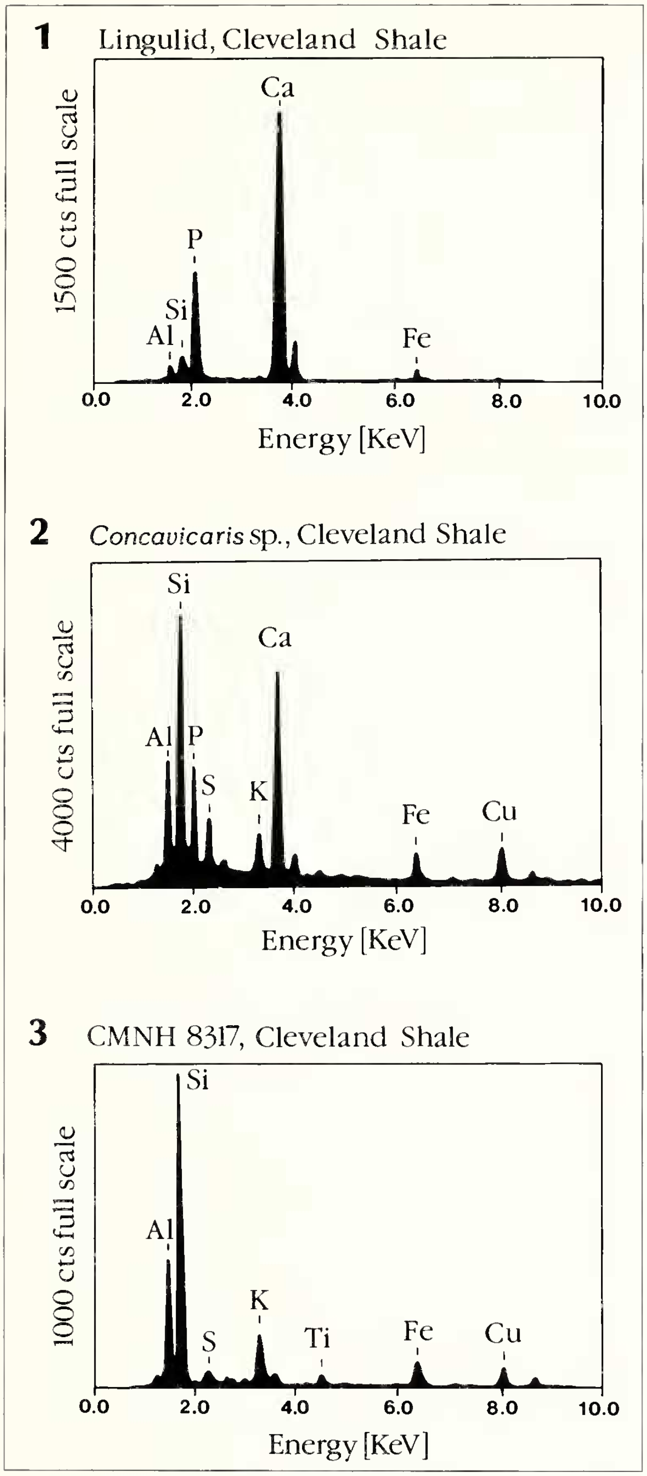

FIGURE 12. *X-ray emission spectra revealing relative composition of some Cleveland Shale specimens. 1, a lingulid brachiopod. 2,* Concavicaris, *a crustacean, CMNH 3740. 3, CMNH 8317, a presumed Devonian anaptychus.*

posterior of rostrum. Superimposed upon fine, concentric ornamentation are broad undulations parallel to ornamentation.

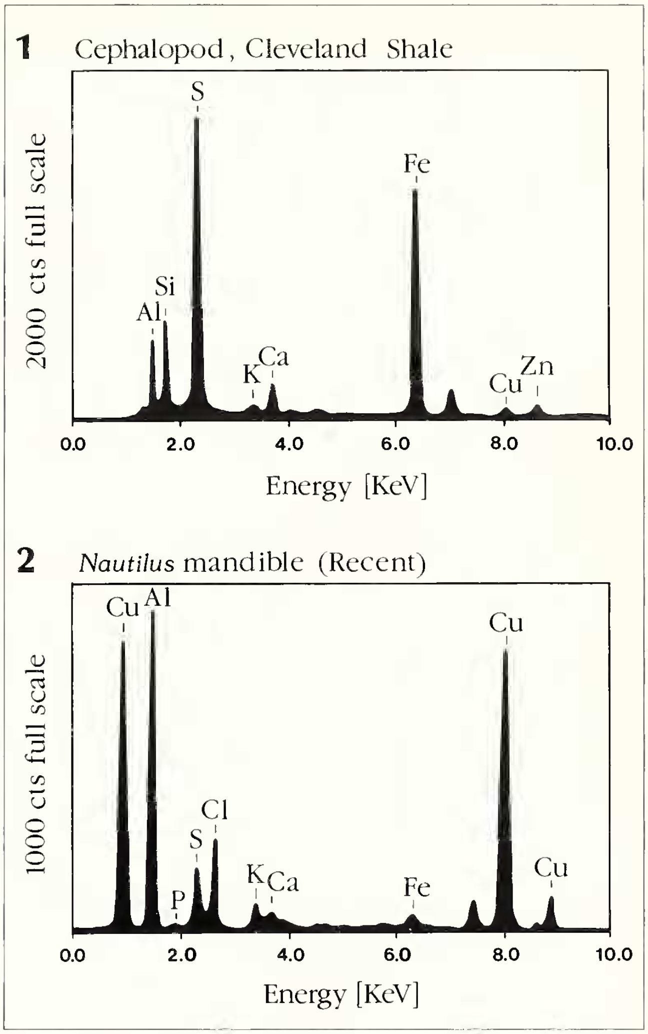

FIGURE 13. *X-ray emission spectra revealing relative composition of 1, an unidentified cephalopod from the Cleveland Shale, CMNH 8705 2, the wing or collar region of the jaw of modern* Nautilus.

Description

Outline nearly elliptical, narrower at rostrum, length 10 to 60 mm, width about two-thirds of length. Surface corrugated in broad concentric undulations subparallel with posterior margin and intersecting lateral margins, spaced about 3 mm apart in a 30 mm specimen. Ornamentation similarly oriented, much more finely spaced, 30-60/cm.

Type

Cooper's holotype of *Spathiocaris ulrichi* was loaned to him by Dr. George H. Girty of the U.S. Geological Survey. It was collected by E.O. Ulrich from the Woodford Formation (Late Devonian) near Dougherty, Oklahoma. It is now at the U.S. National Museum, USNM 112036. The type is 60 mm long and 44 mm wide, somewhat larger than those from the Ohio Shale.

Material

Specimens studied include the holotype; CMNH 8303 and CMNH 8305b, from Big Creek; CMNH 3744 from Chance Creek; and CMNH 8328a and CMNH 8328c, from an unknown locality. All the Ohio specimens are from the Cleveland Shale.

Remarks

Sidetes ulrichi is the single species examined which bears a convex anterior margin. All others have straight or indented margins anteriorly. The dimensions of the specimens studied range from a width-to-length ratio of 0.6 to 0.8; all but the most compacted and flattened exhibit the corrugations superimposed upon the finer concentric ridges. The flattest are assigned to this species primarily on outline and fineness of ornamentation.

Microstructure and Composition

Several of the better preserved specimens, interpreted to be aptychi, were prepared for examination with the scanning electron microscope. The calcareous portions of cephalopod aptychi have a distinctive internal microstructure (Lehmann, 1981). This structure, if identifiable in the fossil specimens, would confirm their identification. The microstructure of authentic arthropod cuticle, and brachiopod and bivalve shells was examined for comparison with the study specimens. Fish scales were eliminated from consideration as those in The Cleveland Museum of Natural History collection from the Late Devonian have morphologies distinctly different from these aptychi (M. Williams, CMNH, personal communication).

An International Scientific Instruments Model SX-40A SEM was used, with an attached Princeton Gamma Tech System 4 Plus energy dispersive x-ray spectrometer. It is routine practice in electron microscopy to coat the surface of the specimen with a conductive material to drain the accumulation of electric charge built up by electron bombardment.

Several of the first specimens examined were coated with gold to a thickness of approximately 500 angstroms, using ISI's P-S1 diode sputter coater. This procedure interfered with the use of the x-ray spectrometer, however. The K-alpha emission line for phosphorous has an energy of 2.014 KeV, while gold has an M-alpha emission line at 2.123 KeV, too close to the phosphorous line to be resolved (Goldstein, et al., 1981). A commonly used alternative is carbon coating, since the emission spectrum of carbon is entirely absorbed by the beryllium window in the detector apparatus. In the absence of a carbon coater, uncoated specimens were examined. This was successful, perhaps due to the high (4.60 ± 1.09 wt.%) average organic carbon content of the Cleveland Shale (Broadhead, et al., 1982), and the carbonaceous nature of the specimens themselves.

Examination of several aptychus specimens revealed no discernable structure remaining within the thin carbonaceous film (Figure 11.1). All thicker regions examined were indistinguishable from the shale matrix and appeared to be molds. It seems that this method of investigation is of little value with material reduced to a carbonaceous film under anaerobic or dysaerobic preservational regimes.

The instrument was used to search for elements that might allow identification of the material composition of the aptychi. Qualitative energy-dispersive X-ray (EDX) spectra were obtained from aptychi and similar appearing fossils and parts from living organisms. The X-ray energy range from 0 to 20 thousand electron volts was scanned, allowing for the detection of nearly all the elements. Only those with atomic number less than berylium were undetectable, as the detector apparatus blocks X-rays from these elements. From the spectra obtained, the relative concentrations of calcium, strontium, and potassium within the samples were used to test for the calcitic, aragonitic, or phosphatic nature of the fossils. Other elements discovered were identified and indicated in the figures. The spectra were compared to test the usefulness of the method in resolving this question.

Inartieulate brachiopods and certain arthropods have long been considered the most likely alternative taxa to which aptychus-like structures might be assigned (Clarke, 1902). Therefore, specimens of a lingulid brachiopod (CMNH uncataloged) and the crustacean *Concavicaris* (CMNH 3740) from the Cleveland Shale were prepared for SEM and EDX examination. Analyses of these specimens and a representative anaptychus, CMNH 8317, are shown in Figure 12. While phosphorous is clearly present in both the phosphatic brachiopod and the crustacean, it is just as clearly absent from the anaptychus. Also conspicuously absent from the anaptychus is calcium or strontium, the latter being a common marker impurity used to identify aragonite (Crick, et al., 1987). It may be impossible to positively identify originally calcareous material from these units, however. Cephalopods tested from the Cleveland Shale, for example the one shown in Figure 13.1, were found to be significantly replaced with pyrite, which can be expected in the metal-rich, anaerobic conditions of deposition (Baird and Brett, 1986). Strontium in particular, present originally in trace amounts, may be undetectable in these altered specimens. The lack of pyrite replacement, common to many shelly fossils in the Cleveland, may suggest that the anaptychi were entirely chitinous in nature, with no mineralized portions.

Modern *Nautilus* mandibles contain phosphorous, but in trace quantities. While the exposed, oral portions of the mandibles are mineralized, the muscle insertion areas are often only lightly calcified if at all, consisting largely of a chitin/protein complex, only thinly coated with aragonite.

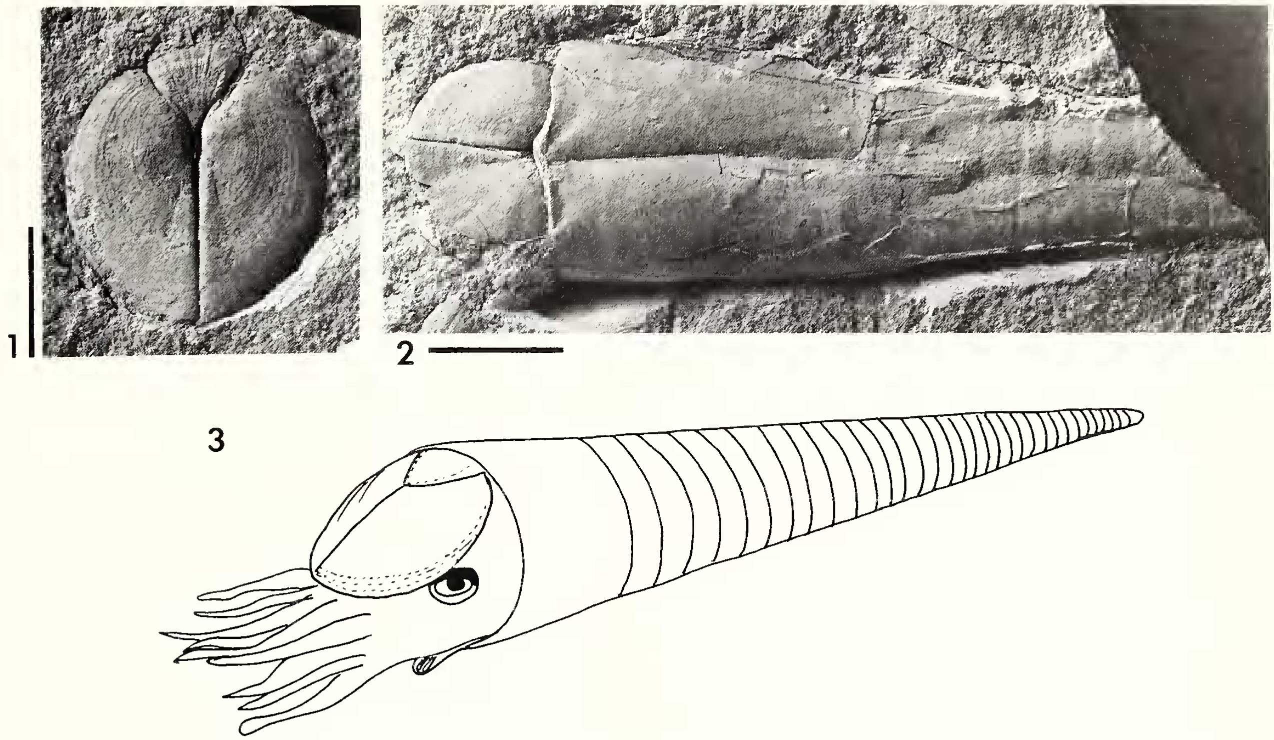

FIGURE 14. Aptychopsis *Barrande, 1872.* 1, *LO 5270 and* 2, *LO 5268, from a Silurian shale quarry in southern Sweden (Stridsberg, 1984). Specimens from the Department of Historical Geology and Palaeontology, University of Lund, Sweden.* 3, *Reconstruction of opercular position of aptychopsid plates in an orthoconic nautiloid, after Turek, 1978.*

This aragonitic layer contains small deposits of brushite, a phosphatic mineral (Lowenstam, et al., 1984; Lowenstam and Weiner, 1989). Total phosphorous content of this posterior region is on the order of 0.30%. This posterior region of the *Nautilus* mandible also reveals little internal microstructure beyond subtle layering, even with SEM examination (Figure 11.2). What structure is seen seems to be an artifact of breakage. The thinness of the jaw specimen allowed for electron beam penetration through it and into the aluminum mounting stub when in the SEM. The X-ray analysis in Figure 13.2 reveals a strong aluminum peak for this reason. The other elements present in the analysis are common trace elements in sea water, and appear to have been incorporated into the structure in significant amounts. Perhaps diagenetic alteration resulted in the depletion of chlorine and enrichment in iron seen in the Cleveland Shale aptychi. The phosphate minerals were shown by Lowenstam, et al. (1984) to be limited to the carbonate layers, which are not present in the Devonian material.

Thus, the x-ray analysis presents evidence denying an arthropod or brachiopod affinity for these fossils. While there are other possible origins for carbonaceous fossil fragments, two of the most likely alternatives based upon the morphology of the fossils are eliminated from consideration. The most parsimonious interpretation is that these are indeed cephalopod aptychi, as suspected by Clarke (1902), Girty (1909), and particularly Ruedemann (1916).

Aspects of Functional Morphology

Historically, when cephalopods were first found with aptychi in place, the approximate match between their outline and the aperture of the conch suggested they served as opercula (Woodward, 1885b; Clarke, 1902; Trauth, 1927). This correspondence is by no means exact, however (Lehmann, 1972, p. 42). Other functions postulated for these structures were as covers for the nidamentary glands or as cartilaginous plates for funnel muscle attachment. Ruedemann (1916, p. 102) suggested the latter, "would naturally also have existed in the Ordovician and Silurian cephalopods..." in attempting to explain the Discinocarida.

This prescient speculation was proven sound by the discovery of specimens of *Aptychopsis* Barrande, 1872 *in situ* in the apertures of orthoconic nautiloids from the Silurian of central Bohemia (Turek, 1978) and southern

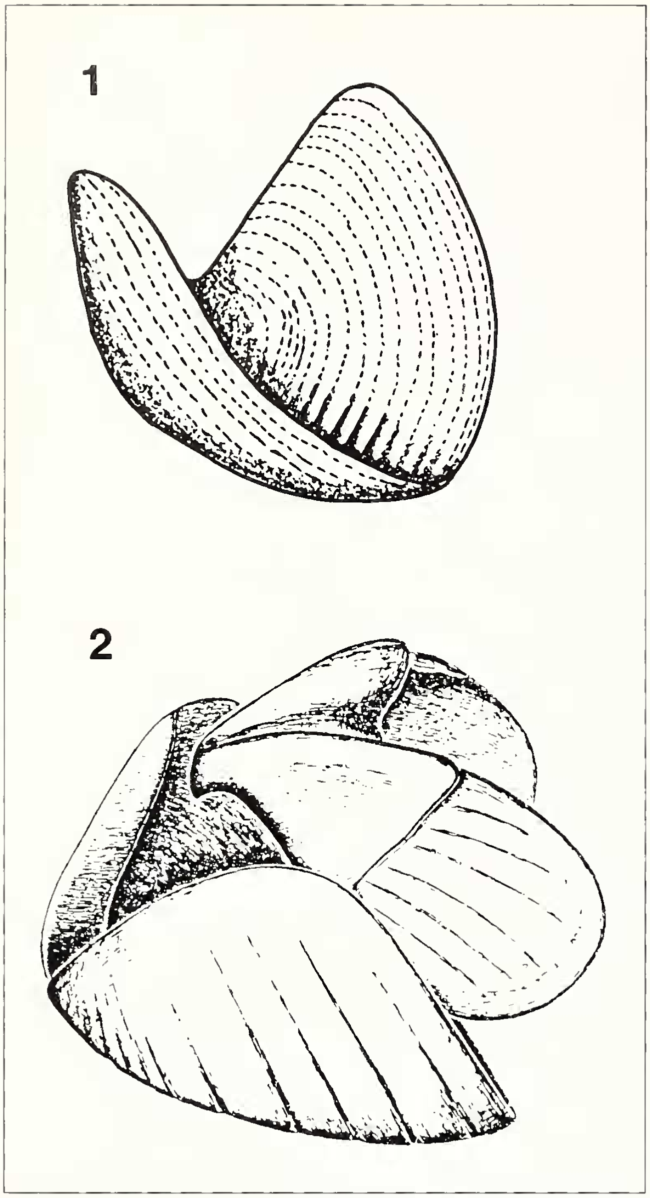

FIGURE 15. *Hypothesized original shapes of aptychi.* 1, *Reconstruction of a Cleveland Shale anaptychus.* 2, *Reconstruction of the mandibles of* Psiloceras, *Hyatt 1867 (from Lehmann 1971.)*

Sweden (Holland, et al., 1978). Aptychopsid plates form a neat, flat circular structure almost precisely fitting the aperture of the nautiloid (Stridsberg, 1984). The three plates involved would be difficult to fold into a concave structure (Figure 14.1). It would seem that these are indeed opercula.

The structures known as aptychi in Mesozoic ammonites seem to have served a different function. Again, discoveries of aptychi *in situ* in cephalopod body chambers provided evidence of their function. These were found to be curved structures, sometimes found associated with an element resembling the upper jaw of *Nautilus* (Lehmànn, 1971, 1972, 1978, 1981; Tanabe, 1983; Tanabe and Fukuda, 1987). It has become accepted by many that these aptychi are the lower jaws of ammonites (Lehmann, 1981; Morton, 1981; Mapes, 1987). One difficulty with this interpretation is the sheer size of the structure, relative to both the upper jaw components and the diameter of the body chamber. In many cases, the aptychus approximates the cross-sectional area of the body chamber. Lehmann's work, cited above, involved serial sectioning of cephalopods, revealing the three-dimensional relationship of the body chamber and its contents, and seems to be the most accurate means of determining the nature of these structures, at least for the Mesozoic ammonites studied.

There are no rigid calcareous plates found with the Devonian fossils, so their preservation as flattened bodies does not necessarily reflect their original morphology. Two specimens of *Sidetes newberryi*, CMNH 8311 and CMNH 8318, exhibit short cracks radiating inward from the posterolateral margin (Figures 9.1, 9.2). These cracks are precisely what would be expected in a convex structure which has been flattened. If this is the origin of the cracks, then closing the gaps should approximate the original form of the structure. As these specimens were folded in half along the medial line, photographs of them were prepared in both normal and reversed orientations. These were then photocopied and enlarged. The resulting reproductions were then cut out and the mirror images were attached along the midline. This caused the paper models to become slightly convex. The cracks along the margin were then cut away and the edges rejoined. This caused the models to assume a broad, scooped shape, similar to that seen in Lehmann's (1970) reconstruction of the jaws of *Psiloceras* from the Jurassic of Germany (Figure 15). Many of the specimens preserved as flattened bodies are folded along the median. In some cases they can be separated from the matrix and studied from both sides, or often the remains of the upper half are preserved along the margins of the extant lower portion (see the arrow in Figure 4.2, *S. emersoni*).

These reconstructions of ammonite jaws (Lehmann, 1970; 1975), suggest to some a scooping, shoveling application rather than a true biting action seen in modern *Nautilus* (Lehmann, 1972), and in other Mesozoic forms (Nixon, 1988). This conclusion is based on the large size of the lower jaws (particularly anaptychi), both relative to the size of the upper jaw and to the total size of the conch. The lack of calcified rostra, or conchorhynchs, to serve as biting surfaces further serves as a basis of interpretation. Calcified beaks have been reported from the Permian (Closs, 1967) and perhaps from the Mississippian (Landman and Davis, 1988), but no older specimens have been found. Where associated upper jaws are of comparable scale, however, it would seem that, even lacking calcified beaks, the jaws could be capable of strong biting action similar to modern coleoids, which lack such calcified surfaces (Tanabe, et al., 1980). The shape of the lower jaw is similar for both applications. Still, the curved shape revealed in the Ohio Shale specimens by these methods, if genuine, fits known jaw structures far better than hypothesized opercula or *Aptychopsis.* We must conclude that these forms of *Sidetes* from the Late Devonian represent cephalopod jaws which have been preserved separately from the animal's conch.

Summary and Conclusion

Approximately 120 specimens of flat, carbonaceous body fossils have been collected from the Cleveland and Chagrin shales of northeastern Ohio. The fossils have been found predominantly in the black Cleveland Shale, which probably represents an anoxic basinal environment (Broadhead, et al., 1982). A few have been collected from the underlying Chagrin Shale, a gray-green unit deposited in dysaerobic conditions (Barron and Ettensohn, 1981; Schwimmer, 1988, Schwimmer and Feldmann, 1990). In addition, specimens housed at the National Museum of Natural History which were collected by Cooper in 1932 have been reevaluated.

These fossils have been identified as representing seven species of *Sidetes* Giebel, 1847, and interpreted to be cephalopod jaw elements. This identification is based upon the general outline of the specimens, and particularly the pattern of ornamentation they exhibit. This concentric pattern of fine ridges is unlike that seen in arthropods, gastropods, bivalves, or brachiopods. Some of the specimens are preserved unfolded and flattened, while others are folded in half along the median line.

Further evidence for this interpretation is furnished by energy dispersive X-ray spectrometry. These fossils show no trace of having once contained phosphorous within the structures studied. It is unlikely that alteration after burial would have so completely removed the element, as both arthropods and inarticulate brachiopods from the same unit have remained phosphatic. On this basis, we can conclude that the *Sidetes* specimens in this study are neither arthropods nor brachiopods.

Two specimens showed signs of compaction damage. When restored to their presumed original shape, they resemble reconstructions of Mesozoic ammonite jaws. It appears that these fossils served the same function in some Devonian cephalopods. By contrast, the Silurian *Aptychopsis* may have been a nautiloid operculum rather than a jaw element.

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